Influences of Earthworms on Biogeochemistry

John M. Blair, Robert W. Parmelee, and Patrick Lavelle

I. Introduction 128
II. Ecological Groupings of Earthworm Species 129
III. Influences on Carbon and Nutrient Fluxes at Different Spatial and Temporal Scales 130
IV. Storage and Turnover of Nutrients in Earthworm Biomass 130
V. Effects of Earthworms at the Microsite Level 132
  A. Earthworm Casts 132
  B. Effects on Microbial Communities, Biomass, and Activity 133
  C. Interactions with Other Soil Invertebrates 136
  D. Influences on Nutrient Transformations and Availability 137
  E. Effects of Earthworms in the Rhizosphere 141
VI. Effects of Earthworms at the Ecosystem Level 143
  A. Soil Organic Matter Dynamics 143
  B. Effects on Plant Productivity 146
  C. Spatial and Temporal Patterns of Nutrient Availability 147
  D. Water and Solute Transport 149
VII. Summary 149
VIII. Research Imperatives 150
  A. Gut Physiology and Biochemistry 151
  B. Functional Groups 151
  C. Native Species 151
  D. Isotope Studies 151
  E. Nutrient Availability 152
  F. Plant Growth 152
  G. Interactions with Soil Biota 152
  H. Spatial Scales 153
  I. Long Term Studies 153
  References 154

1-56670-053-1/95/$0.00+$.50
©1995 by CRC Press, Inc.

I. Introduction

The importance of earthworms in affecting soil structure, organic matter processing and nutrient cycling has long been recognized (Darwin 1881, Edwards and Lofty 1977, Lee 1985). However, there are many areas of earthworm biology and ecology which are insufficiently studied, and the overall effects of these important invertebrates on decomposition and nutrient cycling are still poorly understood (Lavelle 1988). This is particularly true in North America, where soil ecology only recently has begun to receive the degree of attention it has been afforded in Europe, New Zealand, and Australia. Available data on specific aspects of earthworm biology and ecology indicate the potential of earthworms to significantly influence soil structure; organic matter comminution, distribution, and chemistry; soil microbial community structure and activity; soil nutrient transformations (nutrient mineralization/immobilization, N fixation, nitrification, denitrification); plant uptake of nutrients; and potential losses in runoff and soil leachate (see reviews in Edwards and Lofty 1977, Satchell 1983, Lee 1985 and references in the following sections). Additionally, the storage and turnover of nutrients in earthworm biomass is significant in many terrestrial ecosystems. However, in spite of considerable component research on earthworm biology and ecology, critical questions remain unanswered about the effects of earthworms on ecosystem-level processes in both natural ecosystems and agroecosystems in North America.

The present state of knowledge regarding the effects of earthworms on biogeochemical cycling in North American ecosystems is based largely on fragmentary studies done at different locations with different species, and by extrapolating results from other regions of the world. This is due, in part, to the relatively small number of earthworm researchers in North America. Furthermore, there are complicating factors introduced by the effects of glaciation on the present distribution of earthworms, the displacement of native North American earthworm species by introduced species (see Kalisz and Wood, Chapter 5, this volume), and the effects of land use practices on soil communities and processes. With a few exceptions (e.g., Spiers et al. 1986, Parmelee and Crossley 1988, James 1991), the lack of intensive studies of the effects of earthworms in specific ecosystem types in North America is notable, as are the paucity of studies dealing specifically with native North American earthworm species. Within these constraints, we have attempted to construct a general picture of the mechanisms by which earthworms influence the biogeochemistry of North American ecosystems. We have drawn on results of studies done in North America, where possible, and made some inferences about the potential effects of earthworms on nutrient cycling processes based on studies done elsewhere. Our hope is that this approach will point out some areas where earthworms are likely to exhibit significant effects on biogeochemical cycles, and some areas that are in need of further study.

II. Ecological Groupings of Earthworm Species

We preface our discussion by pointing out that the effects of earthworms on biogeochemical processes can vary with different species of earthworm as well as with different soil types, organic matter resources, climatic regimes, and so on (Shaw and Pawluk 1986a, b, Lavelle 1988, Wolters and Joergensen 1992). These differences become important when comparing results from different studies and when extrapolating results from one ecosystem, or region, to another. Three major ecological groupings of earthworms have been defined, based primarily on feeding and burrowing strategies (Bouché 1977). Epigeic species live in or near the surface litter, and feed primarily on coarse particulate organic matter. They are typically small, and have high metabolic and reproductive rates as adaptations to the highly variable environmental conditions at the soil surface. Endogeic species live within the soil profile and feed primarily on soil and associated organic matter (geophages). They generally inhabit temporary burrow systems which are filled with cast material as the earthworms move through the soil. There is evidence that some endogeic species do not feed indiscriminately, but may preferentially ingest soil high in organic matter (James and Cunningham 1989, Judas 1992). Anecic species live in more or less permanent vertical burrow systems which may extend several meters into the soil profile. They feed primarily on surface litter which they pull into their burrows. Some anecic species also may create "middens" at the burrow entrance, consisting of a mixture of cast soil and partially incorporated surface litter.

The habitats and feeding preferences of different earthworm species relate to their potential effects on biogeochemistry. Anecic species, such as *Lumbricus terrestris*, may significantly accelerate the disappearance and breakdown of surface litter, and the macropores created by their burrows may be important in moving water and solutes into lower soil horizons. Their casting activity also may be important in soil profile formation. Geophagous earthworms feed in the soil, but can interact synergistically with anecics. For example, Shaw and Pawluk (1986a) found that *L. terrestris* played a dominant role in controlling decomposition rates in different soil types by mixing surface litter and soil, but this effect was attenuated when geophagous species were included in the soil incubations. This points out the need to consider the effects of entire earthworm communities when evaluating their impact on ecosystem processes. We should also indicate that the ecological categories discussed above are very broad and may not apply equally well to temperate and tropical ecosystems. Refinement of these classifications and questions of functional equivalency of earthworm species in various ecosystems remain to be addressed.

III. Influences on Carbon and Nutrient Fluxes at Different Spatial and Temporal Scales

A better understanding of earthworm influences on biogeochemistry of ecosystems will require studies at a range of spatial and temporal scales. There is ample evidence that effects of earthworms on nutrient cycling processes are highly scale-dependent, and apparently contradictory results may be observed at different levels of spatial and temporal resolution. Therefore, the questions asked and the interpretation of results must explicitly take into consideration the spatiotemporal scales at which the effects of earthworms are measured, including their influences on soil physicochemical properties and their interactions with other soil biota.

Lavelle and Martin (1992) discuss four scales at which effects of earthworms on soil organic matter dynamics are expressed in soils of the humid tropics: (1) gut transit; (2) fresh soil casts; (3) aging casts in the soil; and (4) long-term evolution of the whole soil profile. We believe it would be useful to consider similar scales, and the interrelationships among them, when assessing the potential effects of earthworms on organic matter and nutrient dynamics in temperate, subtropical, and tropical North American ecosystems. However, we need to point out that some important differences exist between the feeding behavior and ecology of tropical and temperate earthworms which may have consequences for how earthworms affect soil formation and processes. The extent to which results from tropical studies can be extrapolated to temperate North American ecosystems is unclear.

An important obstacle to overcome in assessing the net effects of earthworm activity on ecosystem processes involves scaling up from the microsite to the ecosystem level. How are effects measured at the microsite level (casts, burrow walls) related to effects at the whole soil, ecosystem, or landscape level? Our discussion of earthworm influences on biogeochemical processes begins by considering storage and turnover of nutrients in earthworm biomass, a direct effect. We then consider shorter-term effects of earthworm interactions with soils, organic matter and other biota at the microsite level, and discuss potential longer-term effects of earthworm activity at the whole soil level. We conclude with some recommendations for future research on earthworms and biogeochemistry in North America.

IV. Storage and Turnover of Nutrients in Earthworm Biomass

Earthworms play a direct role in the biogeochemistry of many terrestrial ecosystems as carbon and nutrients are accumulated, stored and cycled through earthworm biomass (ingestion, assimilation, respiration/excretion, mortality). Although earthworms can ingest large quantities of organic matter annually

(Edwards and Lofty 1977, Lee 1985), it generally is assumed that their direct contribution to total heterotrophic respiration is small. While earthworm respiration is often the major portion of faunal respiration, it usually is only 5–6% of the total energy flow in terrestrial ecosystems (Lee 1985). The low contribution of earthworms to C flux is due partly to their low C assimilation efficiencies. Estimates of the assimilation efficiencies of endogeic earthworms range from 2–6% to a maximum of 18% (Bolton and Phillipson 1976, Barois et al. 1987, Martin et al. 1992a). Reported assimilation efficiencies of litter-feeding earthworms are highly variable. For example, assimilation of leaf litter by *Lumbricus rubellus* was estimated to be 30–70% depending on the temperature and quality of the litter (Dickschen and Topp 1987). However, Crossley et al. (1971), using a cesium tracer, reported much lower assimilation efficiencies (12–29%) for a number of other earthworm species.

In some ecosystems with high earthworm biomass, and presumably activity, earthworm respiration can represent a significant C flux. For example, Parmelee et al. (1990), in a no-tillage agroecosystem in the southeastern U.S., observed maximum earthworm densities approaching 1000 ind. m^{-2} with a maximum biomass near 30 g ash-free dry mass m^{-2}. Hendrix et al. (1987) constructed a C budget for this system and estimated that during the cool and wet winter-spring season earthworms were responsible for about 30% of total heterotrophic respiration. More field-based estimates of earthworm assimilation, respiration and production in a variety of North American ecosystems are needed to better discern the direct contributions of earthworms to ecosystem carbon flux.

Unlike carbon, it appears that significant amounts of nitrogen move through earthworm biomass in many terrestrial ecosystems. In early work by Satchell (1963), N returned to the soil in dead *L. terrestris* tissue was estimated to be 60–70 kg N ha^{-1} yr^{-1}. When N returned in urine and mucus was included, estimates of total N flux approached 100 kg N ha^{-1} yr^{-1}. Other estimates from New Zealand forests and Polish pastures (reviewed in Lee 1985) also indicate a significant flux of N through earthworm biomass. In North America, Parmelee and Crossley (1988) estimated secondary productivity of the earthworm community in a Georgia no-tillage agroecosystem, and calculated the total N flux through earthworms to be over 60 kg N ha^{-1} yr^{-1}. This is a significant flux of N in this system, equivalent to about 38% of N uptake by the crop. Turnover of N (and C) in earthworm tissue appears to be rapid. Ferriere and Bouché (1985) labelled the anecic earthworm *Nicodrilus longus* by feeding it double labelled (^{14}C and ^{15}N) algae, and determined that the entire C and N content of the earthworm could turnover in as little as 40 days. Barois et al. (1987) incorporated ^{15}N into the tissue of *Pontoscolex corethrurus*, a tropical geophage, and found that 14% of the incorporated ^{15}N was eliminated within 5 days, and 30% was eliminated and replaced within 30 days.

Although the large amount of N moving through earthworm biomass in many systems is striking, it may be of greater significance that earthworm tissue, mucus, and urine are labile and easily assimilable N forms. Satchell (1967) estimated that a minimum of 70% of the N in dead earthworm tissue was mineralized in 10–20 days. Christensen (1988) also noted rapid mineralization from dead earthworms and calculated that 29–42 kg N ha^{-1} was released from dead earthworm tissue during the autumn in a Danish agroecosystem. Nitrogen released from dead earthworms can result in rapid recycling of N on relatively short time scales (Lee 1985). We are unaware of studies where direct fluxes of elements other than C and N through earthworm biomass have been investigated.

In addition to direct turnover of nutrients though their biomass, earthworms can influence biogeochemical processes in a variety of indirect ways. These indirect effects primarily involve interactions of earthworms with soil structure, organic resources, and other soil biota, and have important consequences for both short-term nutrient fluxes and long-term ecosystem dynamics.

V. Effects of Earthworms at the Microsite Level

Many of the most readily measurable, and best documented, effects of earthworms on biogeochemical processes occur at the microsite level. These localized areas which exhibit marked effects of earthworm activity include casts, burrows and middens. Defining the precise area of influence for these microsites can be problematic. While casts and middens may be fairly discrete units, the distance to which effects of earthworm activity extend away from these sites and from burrow walls can be variable. Bouché (1975) defined the drilosphere as the 2 mm-thick zone around the walls of an earthworm burrow. However, the actual area of influence may extend more or less than this depending on the factor being considered. The rhizosphere also is an important site for earthworm-microbe-plant interactions. Most of the effects of earthworms at the microsite scale are a result of combined direct and indirect effects. For example, earthworms may increase N availability in soils directly, by adding excreted N to soil as it passes through the gut or through pores open to the external soil environment, and indirectly by stimulating microbial mineralization of organic soil N in cast material or in the linings of earthworm burrows, or by increasing rates of N fixation.

A. Earthworm Casts

Many studies have demonstrated that earthworm casts have different chemical, biological, and physical characteristics than the bulk soil from which the casts were produced, although the results are sometimes contradictory (Parle 1963, Dkhar and Mishra 1986, Scheu 1987, Wolters and Joergensen 1992). In fact, the specific effects reported in various studies seem to depend on many factors such as earthworm species (Shaw and Pawluk 1986a), soil type and texture (Wolters and Joergensen 1992), soil moisture (Mackay and Kladivko 1985), availability and quality of organic matter (Lavelle et al. 1980, Shipitalo and Protz 1988), and age of the casts at sampling (Scheu 1987, Wolters and

Joergensen 1992). Some studies compare field-collected casts of unspecified age, or broad age intervals, to the surrounding bulk soil (i.e., Tiwari et al. 1989, Dkhar and Mishra 1986, Spiers et al. 1986, Elliott et al. 1990). Others have compared casts produced from homogenized soils in laboratory incubations to control soils without earthworms (i.e., Svensson et al. 1986). Sometimes the casts from these incubations are of a specific age when collected (Scheu 1987, Lavelle et al. 1992) and sometimes they are of mixed ages (Shaw and Pawluk 1986a). Yet other studies have compared the whole soils in which earthworms have been incubated (casts, burrow linings, bulk soil), to soils incubated without earthworms (Wolters and Joergensen 1992, Basker et al. 1992). It is not surprising that these various approaches produce different, and sometimes conflicting, results. Although we have attempted to make some generalizations about how casts and earthworm-worked soil differ from soils not ingested by earthworms, it is important to consider the design of the studies from which results are taken. Of particular importance are the choice of an appropriate reference material, and a time scale relevant to persistence of casts under field conditions (Martin and Marinissen 1993).

B. Effects on Microbial Communities, Biomass, and Activity

Earthworm casts can be important soil microsites with high microbial abundance and activity, and often a different composition, compared to bulk soil. Barois and Lavelle (1986) found that *P. corethrurus* added large quantities of water and easily-assimilable organic matter to soils during transit through the gut, which resulted in large increases in microbial activity in the gut and smaller, but detectable, increases in fresh casts compared to noningested soil. Tiwari et al. (1989) reported higher microbial populations and enzyme activity (dehydrogenase, urease, and phosphatase) in field-collected earthworm casts than in bulk soil (sandy loam Oxisol). Dkhar and Mishra (1986) also reported greater populations of fungi, actinomycetes, and bacteria in field-collected casts than in the surrounding soil. Shaw and Pawluk (1986a) examined the fecal microbiology of an anecic species (*L. terrestris*) and two geophagous species (*Octolasion tyrtaeum* and *Aporrectodea turgida*) maintained in calcareous soils from three different textural classes (sandy loam, clay loam, and silty clay loam) incubated under controlled conditions for one year. At the end of the incubation, casts of *O. tyrtaeum* and *A. turgida* were grouped together and were analyzed separately from those of *L. terrestris*. Shaw and Pawluk (1986a) found that casts of both *L. terrestris* and *O. tyrtaeum*/*A. turgida* had densities of bacteria and actinomycetes which were 1–3 orders of magnitude higher than in control soils from incubation containers without earthworms. Densities of anaerobic microorganisms, filamentous fungi and *Cytophaga* also were higher in casts of both functional groups, although the magnitude of the differences between casts and control soil varied among soil types. Densities of yeasts were greater in casts of both functional groups in the clay loam soil, relative to the control soil, while in the sandy loam and silty clay loam soils only casts of *L. terrestris* exhibited increased densities of yeasts. The differential effects of soil texture on earthworm-induced changes in soil microbial communities under similar incubation conditions is noteworthy, and indicates that earthworm-microbial interactions can vary with soil type. Wolters and Joergensen (1992) also found that the effects of earthworms on soil microbial biomass and activity were highly dependent on soil type and quality of organic resources.

Earthworm-induced changes in microbial populations and activity vary with cast age. Scheu (1987) observed a transient increase in microbial biomass in freshly deposited casts of *Aporrectodea caliginosa*, while older casts supported less microbial biomass than did bulk soil (Figure 1A). Microbial biomass in casts was 128% of that in control soils within 4 h of being egested, and then decreased to approximately 90% of control soils after 2 weeks, and remained at 94% of control soils 30 days after egestion. However, microbial respiration remained elevated throughout the entire incubation, and was 86% higher, on average, in casts than in control soil. The simultaneous increase in respiration and decrease in microbial biomass suggests that casts of *A. caliginosa* may contain a smaller, but more metabolically active, microbial community than does bulk soil. These results are similar to those of Lavelle et al. (1992) for casts of *P. corethrurus* (Figure 1B). They noted a six to seven-fold increase in microbial biomass N in freshly egested casts, relative to noningested soil. However, within 12 h microbial biomass N in the casts had dropped to slightly more than twice the level in controls and then declined only slightly for the remainder of the 16 d incubation. The greater relative increase in microbial biomass observed by Lavelle et al. (1992), compared to Scheu (1987), may be explained in part by differences in organic matter content and microbial biomass of the bulk soils used. Scheu used a forest soil high in organic matter (7.6%) and microbial biomass (1162 μg C g^{-1}), while the soil used by Lavelle et al. was only 1.7% organic matter and supported a much lower microbial biomass (about 100 μg C g^{-1} based on a C:N ratio of 10). It seems likely that additions of labile C during gut passage can cause a transient increase in microbial biomass of fresh casts which is proportionally greater in soils naturally low in organic matter. This observation is supported by studies of the interactions of the tropical geophage *Millsonia anomala* and soluble soil organic matter. In these experiments Lavelle et al. (1980) manipulated the concentration of organic matter in soils fed to *M. anomala* by adding water-soluble organic matter (fresh grass extracts) to a low organic matter soil. Casts of earthworms feeding on soil with low concentrations of soluble organic matter had higher microbial activity than non-ingested soil, while casts of earthworms feeding on soils high in soluble organic matter exhibited decreased microbial activity.

Wolters and Joergensen (1992) also noted some interesting temporal shifts in the effects of earthworms (*A. caliginosa*) on soil microbial biomass and metabolic quotients following cessation of earthworm activity, although they did not isolate fresh casts from surrounding soil in these experiments. They incubated six different soils, with or without earthworms, for 21 days. At the

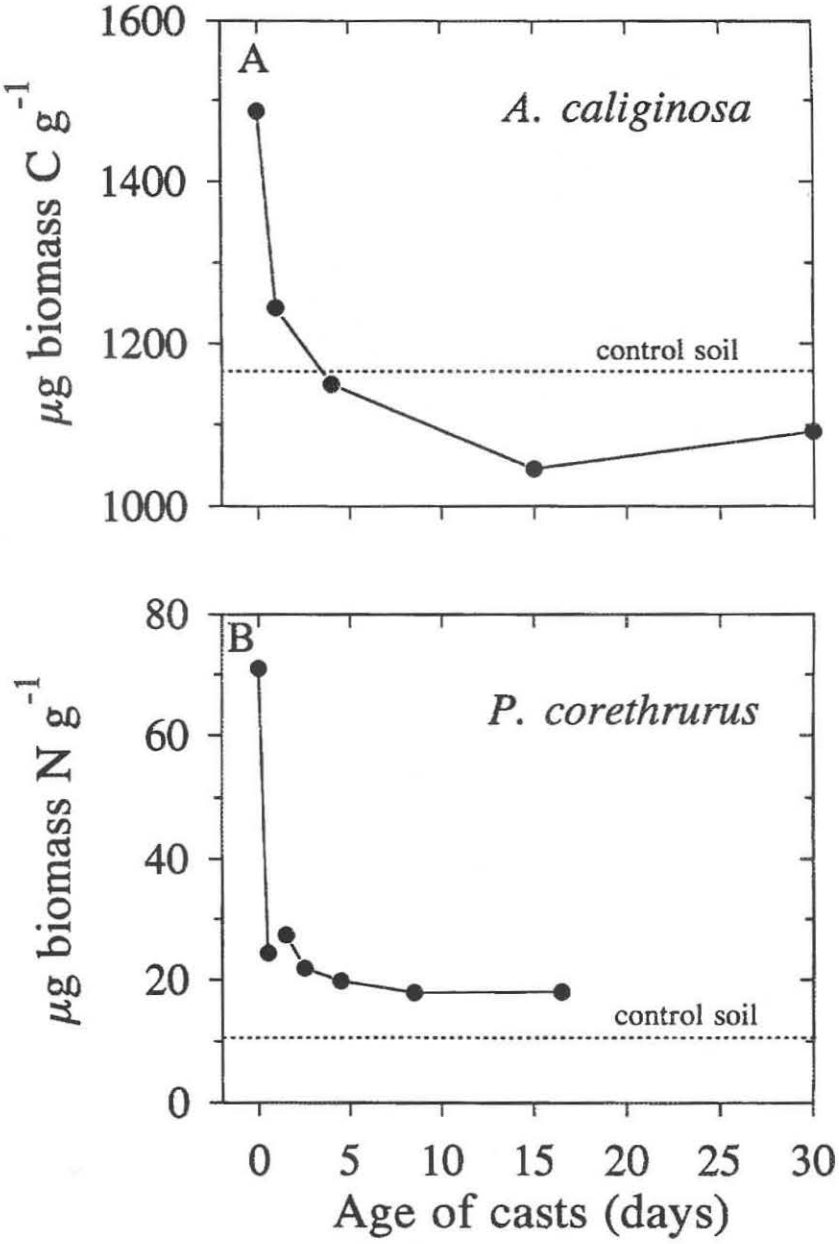

Figure 1. Changes in microbial biomass C over time in casts of *Aporrectodea caliginosa* (Figure 1A; from Scheu 1987) and changes in microbial biomass N over time in casts of *Pontoscolex corethrurus* (Figure 1B; from Lavelle et al. 1992).

end of 21 days microbial biomass and indices of specific metabolic activity (respiration per unit biomass) were measured in a subset of incubation containers, while in another subset of containers, the earthworms were removed and the earthworm-worked soil was incubated for an additional 21 days before measurements were taken. Immediately following the period of earthworm activity (21 days), microbial biomass was lower, relative to controls, in five of the six soils and microbial activity per unit biomass was increased in all soils. Changes in microbial biomass of earthworm-worked soils at 21 days were negatively correlated with initial organic matter content. This is consistent with the results of Lavelle et al. (1980), and with our comparisons of data from Scheu (1987) and Lavelle et al. (1992), providing further evidence that the effects of earthworms on microbial biomass and activity in casts in strongly influenced by organic matter content of the ingested soil. In contrast, Wolter and Joergensen (1992) found that the effects following cessation of earthworm activity and additional incubation (42 days) were highly soil specific, often were the opposite of those measured while earthworms were still active, and were not related to initial soil variables. Wolters and Joergensen (1992) speculate that the depression of microbial biomass and increase in specific microbial activity sometimes observed in fresh casts are due to an increase in the relative importance of bacteria and actinomycetes which can quickly mineralize labile organic substrates in fresh casts. As casts age, labile substrates are exhausted and fungi may become relatively more important, resulting in increased microbial immobilization of C and N, and a lower specific metabolic activity. The soil-specific, resource-specific, and time-dependent nature of microbial responses to earthworm activity may be responsible for some of the apparently conflicting results of various published studies of earthworm-microbial interactions.

One of the greatest impacts of macroinvertebrates, including earthworms, on microbial decomposers may be to alter fungal:bacterial ratios at a scale relevant to processes in the field (Anderson 1988). Potential changes, caused by earthworms, in relative proportions of soil fungi and bacteria are important because of differences in C assimilation efficiencies of fungi and bacteria (Adu and Oades 1978), and production of more recalcitrant organic substances by fungi which may affect soil organic matter (SOM) storage. However, most evidence for earthworm-induced changes in microbial community structure and activity comes from comparisons of fresh casts with control soils or from laboratory incubations of earthworms in small volumes of soil. The extent to which such effects occur in bulk soils in the field remains to be investigated, as does their functional significance.

C. Interactions with Other Soil Invertebrates

It seems reasonable to conclude that earthworm-induced changes in the microbial community will affect higher trophic levels in the soil food web, and the potential importance of earthworms in affecting populations of other invertebrates has been noted (Coleman 1985), but remains largely uninvestigated. Earthworms may affect other soil-inhabiting invertebrates by altering their resource base (amount and distribution of organic matter and microbial populations), by affecting soil structure (porosity, aggregate structure), by direct ingestion, and by dispersal. Alteration of the soil environment in microsites such as earthworm middens can affect the distribution of soil invertebrates in some ecosystems. Middens differ from surrounding soil in moisture content, water holding capacity, nutrient status, and microbial composition and activity. Hamilton and Sillman (1989), found differences in the microarthropod communities associated with middens in fields and woodlots, and suggested that middens contribute substantially to spatial variability in the distribution of soil microarthropods. Marinissen and Bok (1988) reported that larger species of Collembola, and larger individuals within a species, occurred in Dutch polders that had been colonized by earthworms, compared to those without earthworms. They attributed this to the presence of greater numbers of large pore spaces in the presence of earthworms, although other factors such as distribution of organic matter also may have been important. Earthworms are capable of digesting ingested protozoa (Bamforth 1988), and may also affect nematode populations by ingestion (Ellenby 1945, Dash et al. 1980) or by dispersion (Shapiro et al. 1993). Shapiro et al. (1993) observed enhanced vertical dispersal of the entomopathogenic nematode *Steinernema carpcapsae* in the presence of *L. terrestris* and *Aporrectodea trapezoides*. They noted the presence of nematodes on the exterior and interior of earthworms and suggested that transport by earthworms may increase dispersal of entomopathogenic nematodes in soil. Earthworms introduced into New Zealand pastures reduced total nematode numbers by 37–66% (Yeates 1981). Although the generic composition of the nematode community was unchanged, populations of bacterial feeders and fungal-feeding Tylenchida were decreased in the presence of earthworms. This may have been due to ingestion of free-living nematodes by earthworms or may reflect changes in the soil microbial community caused by earthworms. Unfortunately, there are few studies that have examined the effects of earthworms on other soil invertebrate groups and on populations and activity of soil microorganisms concurrently. Earthworm-induced changes in the decomposer community may affect decomposition and nutrient cycling processes and are in need of further investigation.

D. Influences on Nutrient Transformations and Availability

Availability of nutrients (C, N, P, K, Ca) in earthworm casts and burrow walls is generally higher than in bulk soils, and many studies have indicated that earthworm casts and burrows are important microsites for some specific nutrient transformations. The quantity, form, and distribution of C in earthworm casts and burrow linings is often quite different than in bulk soil. Lee (1985) reviewed data from a number of studies comparing casts to bulk soils and found consistently higher quantities of C in casts. In a heterogenous soil environment, some of this effect can be attributed to selective feeding and preferential ingestion of soil higher in organic matter. However, it also is clear that earthworm feeding can modify the form and distribution of ingested organic matter. Barois and Lavelle (1986) examined some of the physicochemical changes that occur in the earthworm gut and noted marked changes in concentrations of water-soluble organic compounds during soil transit. They suggested that addition of readily-assimilable organic compounds during passage through the earthworm gut results in increased microbial degradation of more complex organic substrates in the soils. This "mutualistic digestive system" has been proposed for both tropical (Barois and Lavelle 1986, Barois 1992) and temperate (Trigo and Lavelle 1993) earthworm species. The form of carbon in casts also can be different than in bulk soil. Martin (1991) found that *M. anomala* reduced the coarse organic matter fraction (250–2000 μm) in fresh casts, relative to bulk soil, as a result of comminution of ingested organic matter. Shaw and Pawluk (1986a, b) reported greater amounts of clay-associated C in earthworm casts than in bulk soil, suggesting that earthworms may promote stabilization of soil C by promoting binding with clays.

Earthworms can significantly affect N transformations in casts and burrow walls. Levels of inorganic N are often quite high in fresh earthworm casts, with ammonium being the dominant form (Scheu 1987, Lavelle et al. 1992). However, nitrification usually occurs rapidly in casts, and several authors have noted a simultaneous decline in ammonium concentrations and increase in nitrate concentrations as casts age (Parle 1963, Syers et al. 1979). Lavelle et al. (1992), in studies with *P. corethrurus*, found that inorganic N concentrations in fresh casts were approximately five times greater than in non-ingested soil, with the greatest change occurring in ammonium concentrations (Figure 2). Concentrations of microbial biomass N in casts also were 6–7 times greater than in control soil. As the casts aged there was a rapid decline (approximately 50%) in concentrations of inorganic + microbial biomass N within the first 12 hours. For the remainder of the 16 d incubation, ammonium levels continued to decline, while nitrate levels increased. The increase in inorganic N concentration in casts, relative to non-ingested soils, is a combined result of excretion of ammonia into soil as it passes through the gut and increased microbial mineralization of organic N. The cause of the rapid decline in labile N in fresh casts is unknown, although ammonia volatilization and denitrification may be important and should be further investigated.

Relatively little is known regarding the effects of earthworms on gaseous N fluxes, although there is evidence that casts and burrow walls may be important microsites for both losses (denitrification, volatilization) and inputs (N-fixation). The combination of increased nitrate and organic C, soil aggregation, and microbial activity in casts can lead to conditions favorable for denitrification (Svensson et al. 1986). Elliott et al. (1990, 1991) compared denitrification rates from earthworm casts and bulk clay loam soil collected from fertilized and

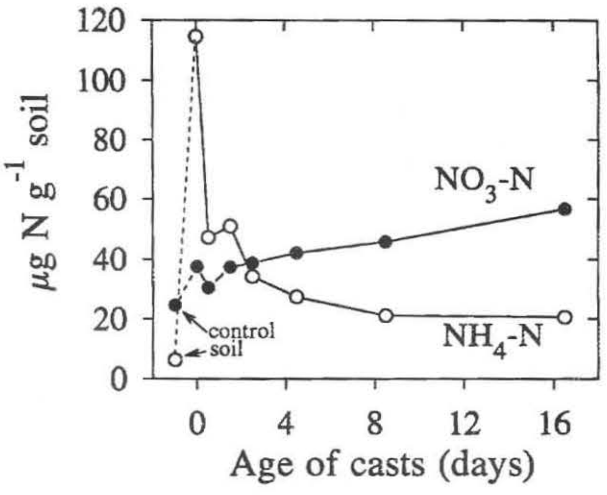

Figure 2. Temporal changes in concentrations of ammonium and nitrate nitrogen in aging casts of *Pontoscolex corethrurus* fed on an Amazonian Ultisol (from Lavelle et al. 1992).

unfertilized English pastures which were drained or undrained. They found consistently higher rates of denitrification in casts, compared to bulk soil samples, and concluded that earthworm casts are important microsites for denitrification and contribute to the spatial heterogeneity of denitrification measurements in the field. Knight et al. (1992) summarized the differences in N_2O production rates of casts and soils (Figure 3), and used these values together with data on annual rates of cast production to estimate annual denitrification rates from surface casts and bulk soils in these pastures. They estimated that surface casts could contribute from 12–26% of total denitrification annually.

In addition to the potential importance of casts as sites for gaseous loss of N, there also have been reports of earthworm activity increasing N-fixation rates. For example, Shaw and Pawluk (1986a) reported higher levels of acetylene reduction (an indication of N-fixation activity) by *Spirillum* sp. in burrow linings of *L. terrestris*, than in control soils. Bhatnagar (1975, reviewed in Lee 1985) reported that about 40% of the total aerobic N-fixers, 13% of the anaerobic N-fixers, and 16% of the denitrifying bacteria in the soil occurred within the 2 mm zone surrounding earthworm burrows (the drilosphere). Other studies also have suggested increased N fixation in the earthworm gut and/or casts (Spiers et al. 1986, Barois et al. 1987, Šimek and Pižl 1991). However, the extent to which earthworms enhance N fixation, and the potential significance of this phenomenon, remains debatable (Lee 1985) and needs further investigation.

Phosphorus availability in casts is often significantly greater than in bulk soils (Sharpley and Syers 1976, Tiwari et al. 1989, Krishnamoorthy 1990). In a U.S.

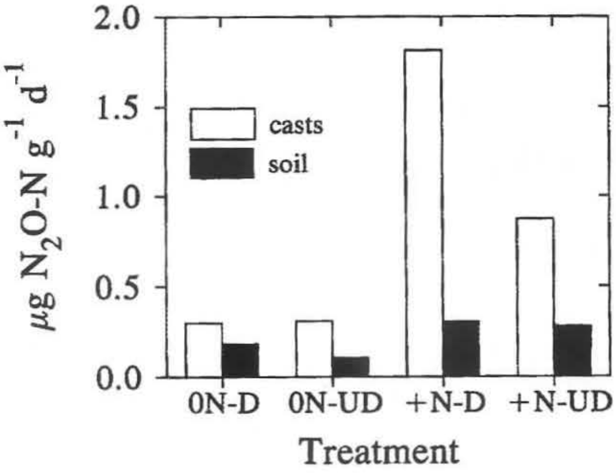

Figure 3. Mean rates of denitrification, expressed as nitrous oxide production, in field-collected casts and bulk soils of English pastures. Treatments are no fertilizer (0N) or 200 kg N ha^{-1} yr^{-1} (+N) and drained (D) or undrained (UD) (from Knight et al. 1992).

agroecosystem, Lunt and Jacobson (1944) reported that extractable P was 150 μg g^{-1} in casts, as opposed to 21 μg g^{-1} in bulk soil. James (1991) found that extractable P in surface casts of earthworms in a North American tallgrass prairie ecosystem usually ranged from 18–30 μg P g^{-1}, while bulk soils were in the range 3–10 μg P g^{-1}. Based on additions of C, N, and P to bulk soil, casts and burrow walls of *A. caliginosa*, Scheu (1987) concluded that P was less limiting to microbial activity in freshly deposited casts than in bulk soil or soil from burrow walls. However, P limitations tended to increase as casts aged, and this was reflected by a decrease in amounts of bicarbonate extractable P from 13.2 μg P g^{-1} in fresh casts to 7.6 μg P g^{-1} in 15-day-old casts. Increased P availability in fresh earthworm casts has been attributed to an increase in phosphatase activity in egested material (Satchell and Martin 1984), although it remains unclear to what extent the increased phosphatase activity is due directly to earthworm-derived enzymes, as opposed to increased microbial activity (Park et al. 1992). Other studies suggest that gut passage also alters the P-sorption capacities of some tropical soils (Lopez-Hernandez et al. 1993).

Earthworm activity may significantly affect calcium availability in soils. Many species of earthworms possess calciferous glands or esophageal regions which are involved in production of $CaCO_3$ spherules. Spiers et al. (1986) reported that a native North American earthworm in the genus *Arctiostrotus*, which occurs in the wet coastal forests of Vancouver Island, can convert calcium oxalate crystals on ingested fungal hyphae to calcium bicarbonate, which then is egested in cast material. This temporarily increases calcium availability in the fresh casts, and increases pH which could affect concentrations of other soluble nutrients available for plant uptake. Amounts of extractable potassium also have been reported to be elevated in earthworm casts, relative to bulk soils (Tiwari et al. 1989). In a laboratory experiment in which two individuals of *A. caliginosa* were maintained in 30 g of silt loam soil, Basker et al. (1992) found that earthworm activity increased the proportion of total soil potassium in exchangeable form, presumably by shifting the equilibrium between exchangeable and non-exchangeable forms in the soil.

E. Effects of Earthworms in the Rhizosphere

The rhizosphere is another microsite where earthworms may have strong effects on nutrient cycling processes through their interactions with plant roots and rhizosphere microbes. Although there are few data available on earthworm-rhizosphere interactions, there appears to be potential for synergistic effects of root and earthworm activity on nutrient mineralization and plant uptake processes. Plant roots and earthworms affect soil structure, chemistry and microbial activity in similar ways. Both create new pores in the soil matrix, can increase soil aggregate stability, secrete labile low molecular weight C compounds, and can stimulate microbial activity. A key factor in earthworm-rhizosphere interactions could be the secretion of available or readily mineralizable N in earthworm mucus and casts. There have been few studies to determine if earthworm activity is greater in the rhizosphere than in bulk soil, but earthworm secretion of N in the rhizosphere would be available for root uptake with potential effects on plant production.

James and Seastedt (1986) present evidence for an earthworm-rhizosphere effect on N dynamics. They observed increased root biomass and lower levels of NO_3-N in leachate when *Diplocardia* spp. were present compared to pots without worms. They hypothesized that localized N mineralization in the rhizosphere may have increased plant uptake of N, contributing to both increased root growth and decreased N leaching. Spain et al. (1992) also provide evidence that earthworms increase plant production, and that the increased growth is associated with increased uptake of N and P in the presence of earthworms. They found positive correlations between earthworm biomass (*M. anomala* and two eudrilid species) and final plant biomass, and concentrations of N and P in plant roots. When microbial biomass was labelled with ^{15}N, earthworms increased the transfer of ^{15}N to both foliage and roots (Figure 4), suggesting that enhanced mineralization of N from microbial biomass in the rhizosphere could increase plant uptake. The ability of roots to utilize nutrients in earthworm casts has also been observed circumstantially by Spiers et al. (1986), who noted that live fine and very fine roots were concentrated in fresh casts of *Arctiostrotus* sp. in a Vancouver Island coastal forest.

Earthworms also may affect nutrient dynamics in the rhizosphere by consumption of live and/or dead roots. The importance of root consumption by earthworms rarely has been explored, but there is some evidence that both live and dead roots are ingested. James and Cunningham (1989) found root fragments among the gut contents of all seven species examined from a tallgrass prairie. With the exception of one species, the organic matter concentrations of the gut contents were nearly twice that of bulk soil, leading James and Cunningham (1989) to speculate that these worms were feeding preferentially in organically enriched sites and that well-decomposed material in the rhizosphere may be a preferred substrate. Whether or not earthworms consume live roots remains controversial, but there is some evidence this does occur. Cortez and Bouché (1992) used short-term labelling of rye-grass to enrich roots with ^{14}C. After 24 h of contact with plant roots, they found that gut contents of *L. terrestris* were labelled with ^{14}C and concluded that the worms had fed on root tissue. However, gut contents were not examined for root fragments and it was not possible to conclude definitively the existence of herbivory in earthworms. In a field experiment in which clover roots were labelled with ^{32}P applied to the foliage of the clover plants, Baylis et al. (1986) found high levels of ^{32}P in three species of earthworms after a six hour labelling period, suggesting that live root consumption occurred. The magnitude and potential significance of live-root feeding by earthworms will require further study.

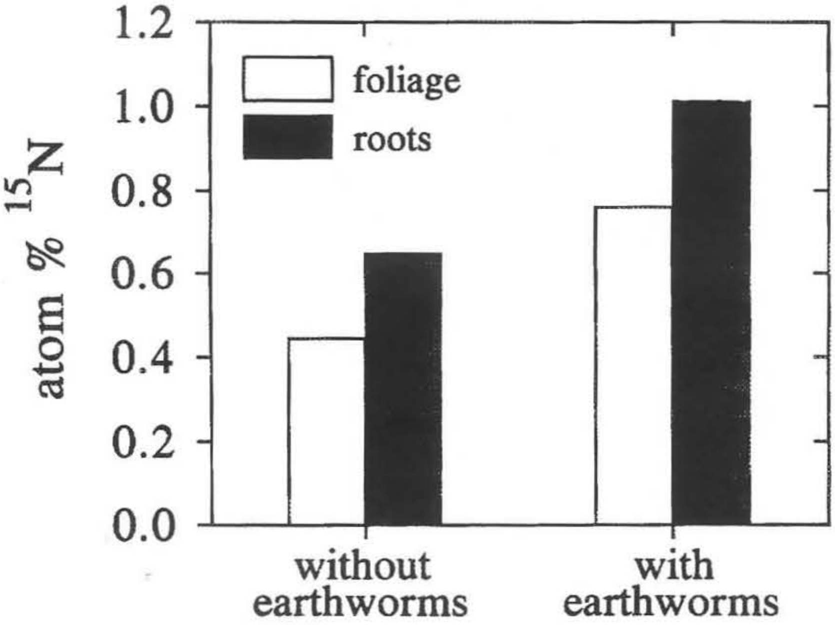

Figure 4. Effects of the earthworm *Milsonia anomala* on transfer of ^{15}N from soil microbial biomass to plants grown in an infertile savanna soil (from Spain et al. 1992).

VI. Effects of Earthworms at the Ecosystem Level

The effects of earthworms on whole soil structure and function, and ecosystem-level nutrient fluxes, are less well understood than their effects at the microsite level. Some important research questions at this scale center on discerning the net effects of earthworms on soil structural development, storage and forms of soil organic matter and nutrients, influences of earthworm-induced macropores on fluxes of water and materials, and ecosystem-level estimates of nutrient inputs, retention, and losses.

Earthworms, through their burrowing and casting activities, turn over tremendous quantities of soil on an annual basis, and can induce major structural changes in soil which have important consequences for both water and nutrient fluxes. Soils with high populations of earthworms often have a greater number and altered size distribution of stable soil aggregates, greater porosity, higher infiltration rates, and less surface litter than soils without earthworms. Changes in soil aggregate structure and macropore densities and distribution may have significant effects on carbon and nutrient storage and movement in soils. In this section we focus on the effects of earthworms on soil organic matter dynamics, stable aggregate formation and its relationship to organic matter dynamics, the potential for earthworms to alter patterns and timing of nutrient availability, and the effects of earthworm-induced macropores on water and solute movement.

A. Soil Organic Matter Dynamics

A fundamental question involving the effects of earthworms on soil organic matter is the extent to which they are able to utilize different organic matter fractions of the bulk soil. Earthworms ingest a range of organic matter fractions when feeding, but may differentially assimilate C from these various fractions. Martin et al. (1992a) used soils in which specific size classes were replaced with like size classes differentially labelled with ^{13}C, and found that *M. anomala*, a tropical geophage, assimilated soil organic matter from both large (250–2000 μm) size classes, considered to include newer plant-derived organic matter, and small (0–20 μm) size classes thought to comprise older clay-associated organic matter. However, other research utilizing $\delta^{13}C$ values of earthworms living in soils with differentially labelled organic pools has indicated that earthworms assimilate C primarily from young soil organic matter pools (Martin et al. 1992b). It appears that earthworms assimilate more readily decomposable organic substrates of the same age distribution utilized by the overall decomposer community. This seems to be true for both litter-feeding and geophagous species. Although geophages may ingest large quantities of older, humified organic matter, they apparently assimilate more C from the younger more labile fractions. These results are based, in part, on studies done in a temperate agroecosystem in France, and may apply to temperate ecosystems in North America, although this remains to be investigated.

In spite of their apparent propensity to utilize organic matter pools of similar age (Martin et al. 1992b), different species, or at least functional groups, of earthworms may have disparate effects on organic matter dynamics. Shaw and Pawluk (1986a) suggest that the effect of geophages in different soils is to enhance trends in decomposition which are already dictated by soil type, while anecic species, such as *L. terrestris*, may play a more prevalent role in modifying organic matter decomposition rates in different soils by removing surface litter and mixing it with mineral soil. A common perception is that earthworms, particularly anecic species, tend to increase organic matter decomposition rates. However, Shaw and Pawluk (1986a) found reduced decomposition rates of grass added to a sandy loam soil (lower soil respiration and greater increases in total soil C) in the presence of *L. terrestris*, relative to control soils or those where only geophages were present. The net effect was an increase in the fraction of C associated with the clay-bound fraction and a net increase in soil organic matter storage. In the same experiment, *L. terrestris* had the opposite effect on C dynamics in clay loam and silty clay loam soils, where decomposition of added grass residues was significantly accelerated.

One of the most basic unanswered questions regarding the effects of earthworms on soil organic matter dynamics is whether the net effect of earthworm activity is, in the long term, to increase rates of organic matter decomposition or to promote soil organic matter storage. There are numerous studies demonstrating accelerated breakdown of coarse particulate organic matter as a result of earthworm activity. For example, Mackay and Kladivko (1985) conducted a pot study in which soybean and maize residues were added to a Raub silt loam from Indiana with different densities of *L. rubellus*, and found that earthworms significantly decreased the amount of residue >300 μm recovered from the pots. Zachmann and Linden (1989) also observed lower recoveries of corn residues added to a Waukegan silt loam in Minnesota in the presence of *L. rubellus*. Parmelee et al. (1990), in a biocide field experiment in Georgia, found that reducing earthworm populations in conventional and no-tillage agroecosystems (Typic Rhodudult, Hiwassee sandy clay loam) resulted in increased standing stocks of both fine (790–2380 μm) and coarse (>2380 μm) particulate organic matter in the no-tillage system and coarse particulate organic matter in the conventional tillage system.

However, other recent research has suggested that stabilization of organic matter in earthworm casts may result in long-term reductions in mineralization of organic matter in some tropical soils, raising important questions about the long-term net effects of earthworms on soil organic matter pools. Martin (1991) examined the effects of the tropical geophagous earthworm *M. anomala* on soil organic matter dynamics over different time scales. In these experiments earthworms were maintained in homogenized and sieved soil. Fresh casts were compared to noningested soils to determine the short-term effects of soil ingestion on organic matter pools. Subsamples of collected casts then were placed in culture boxes and incubated for up to 420 days at constant temperature and moisture to determine the longer-term effects of feeding and cast production

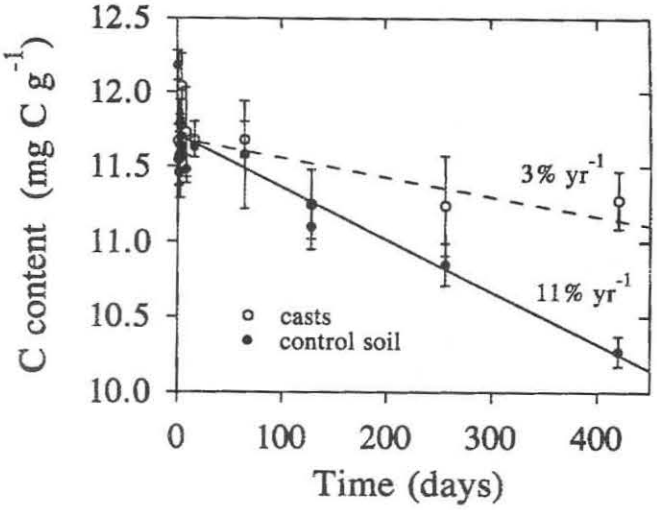

Figure 5. Changes in the C content of casts of *Milsonia anomala* and of unaggregated control soil (2 mm sieved) during 420 days of incubation at 15% moisture and 28°C (from Martin 1992).

on retention of carbon. Short-term effects of earthworm feeding included a significant reduction of organic matter contained in particle-size fractions between 250 and 2000 μm, and a 2% decline in total C content, suggesting that, in the short term, *M. anomala* increases comminution and mineralization of organic matter. However, the longer-term incubations of casts and control soils (Figure 5) revealed much lower C mineralization from the casts (3% yr^{-1}), than from the nonaggregated control soils (11% yr^{-1}). The reduction in C mineralization was attributed to increased protection of organic matter in stable soil aggregates created by earthworm casting. This may be an important mechanism for organic matter stabilization in tropical soils where abiotic factors (climate and soil texture) favor rapid C mineralization (Lavelle and Martin 1992).

The extent to which earthworms can increase protection of organic matter in temperate soils is largely unknown. There are conflicting data, including some from North America, regarding the effects of earthworms on formation and persistence of stable soil aggregates in temperate soils. Mackay and Kladivko (1985) reported that *L. rubellus* significantly increased the water stability of moist soil aggregates in a Raub silt loam soil incubated with or without crop residues. However, this effect was not apparent when soils were air-dried and rewetted. Shipitalo and Protz (1988) found that clay dispersability of fresh casts was greater than that of bulk soil, but aging increased stability of casts. They also provide data suggesting that the quality of organic matter ingested is a determinant of cast stability. West et al. (1991) showed that *L. rubellus* increased the proportion of water-stable aggregates in the size fraction >2 mm and decreased the proportion between 0.25 and 2 mm in laboratory incubations with two Ultisols from the Georgia Piedmont. The effect was greater in a Cecil loamy sand than in a Pacolet sandy clay loam. Preliminary data from an experiment in Ohio in which earthworm populations are being manipulated (reduced, enhanced, unmanipulated) in field enclosures (Blair et al. in press) suggests that earthworms can affect the stability of soil aggregates under field conditions (Ketterings 1992). Data from the first year of the experiment show that experimental increases in earthworm populations resulted in increased water-stability of aggregates in the three largest size classes examined (1–2, 2–4, and 4–10 mm). Earthworm reductions decreased the proportion of water-stable aggregates in the largest size class only. The increase in the proportion of large water-stable aggregates under enhanced earthworm populations was associated with increased C and N content of the aggregates. Further long-term studies are needed to determine the extent to which earthworms influence the production and distribution of water-stable soil aggregates and the impact this has on soil organic matter dynamics in North American soils. Two important considerations are the form of the casts (compact or slurries) and the time scales over which they persist in the field.

B. Effects on Plant Productivity

Net soil organic matter accumulation or degradation depends on the balance between production and decomposition. Most of our discussion so far has focused on the potential of earthworms to alter soil organic matter dynamics by influencing decomposition and mineralization processes (comminution, redistribution, aggregate formation, physical protection). However, the potential of earthworms to affect plant production, and rates of organic inputs, also should be considered. There are data indicating that earthworms can increase plant productivity in pot experiments (i.e., Hopp and Slater 1949, Spain et al. 1992), although this effect has not been observed in all experiments (i.e., Mackay and Kladivko 1985, James and Seastedt 1986). There are fewer data regarding the effects of earthworms on plant productivity under field conditions, although a stimulatory effect has been noted in earthworm introduction experiments in New Zealand pastures (Stockdill 1982) and reclaimed Dutch polders (Hoogerkamp et al. 1983). Earthworms may influence plant growth by altering physical characteristics of the soil and soil nutrient availability. In addition, several studies have pointed to the presence of growth regulating substances in earthworm casts as a possible mechanism affecting plant growth (Nielson 1965, Atlavinyte and Dačiulyte 1969, Springett and Syers 1979, Krishnamoorthy and Vajranabhaiah 1986), although the specific effects of these substances, and their relationships with plant productivity in the field, are still not well understood (Tomati et al. 1988).

C. Spatial and Temporal Patterns of Nutrient Availability

In earlier sections we considered the effects of earthworms on nutrient availability in specific microsites (i.e., casts). Relating these microsite effects to measurable changes in nutrient availability in bulk soils and ecosystem-level nutrient cycling processes is a formidable challenge. Earthworm activities appear to have the potential to alter patterns and timing of nutrient availability, particularly in temperate ecosystems where earthworm activity exhibits a definite seasonality. We suggest that an important effect of earthworms may be to alter patterns of microbial mineralization-immobilization, although this does not appear to have been examined in detail. In a study of N dynamics in earthworm casts in a New Zealand pasture, Syers et al. (1979) found that the production of surface casts (predominantly from *L. rubellus*,) and concentrations of C, total N, and inorganic N in the casts, followed clear seasonal patterns. Peak total N and C content of casts coincided with peak litter production. Concentrations of ammonium in the casts at the beginning of the casting season (April) were approximately 80 μg N g^{-1}, but dropped to 55 μg N g^{-1} by mid May. Concentrations of ammonium then increased to a peak of about 115 μg N g^{-1} in August, before declining to a level similar to that at the start of the study. Changes in nitrate concentration were inversely related to ammonium during this period and increased from about 25 to 48 μg N g^{-1}. These patterns appear to be more closely related to cast production and litter removal, than to seasonal variation in soil nutrient pools. Although the accumulation of inorganic N in casts is small (3.5 kg N ha^{-1} yr^{-1}) compared to total system turnover of N, timing and spatial distribution of this N may magnify its importance. James (1991), found that the N and P content of surface casts of earthworms in North American tallgrass prairie ecosystems also varied seasonally. Ammonium and extractable P concentrations were higher in the spring and fall than in midsummer (Figure 6). Such combinations of higher casting rates and greater concentrations of extractable N and P in the spring and fall could alter patterns of N and P availability, although the magnitude of this effect and its potential importance for nutrient cycling and retention are unknown.

In addition to differences in seasonal cast production, Wolters and Joergensen (1992) suggest another mechanism by which earthworms could influence patterns of N mineralization and immobilization. They found that ongoing earthworm activity reduced soil microbial biomass, and therefore microbial immobilization of N. However, as earthworm-worked soil aged following the cessation of earthworm activity, N immobilization in microbial biomass increased in at least some soil types, suggesting the possibility of enhanced N mineralization coinciding with seasonal periods of earthworm activity and increased immobilization as earthworms become inactive. We suggest that further studies of temporal shifts in nutrient availability in response to earthworm activity, in a variety of terrestrial ecosystems, are essential for understanding the influence of earthworms on biogeochemical processes at the ecosystem level.

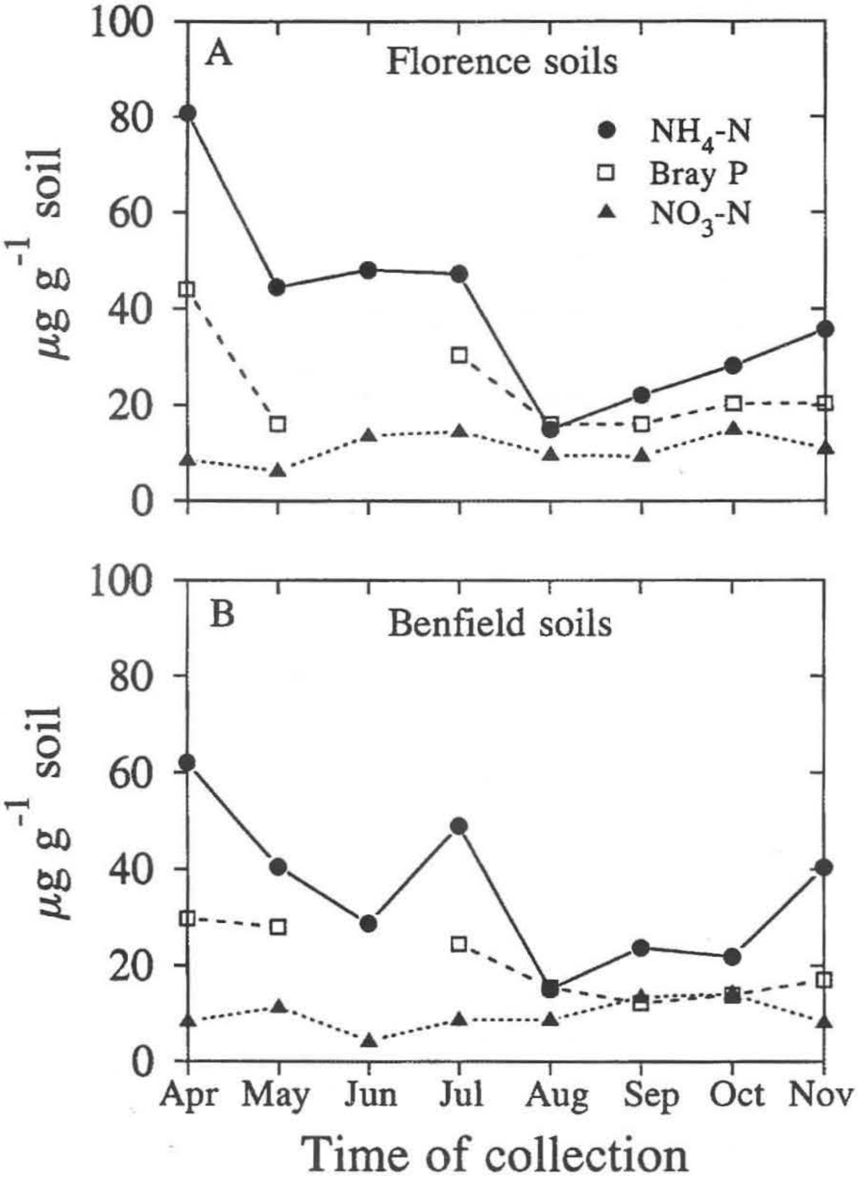

Figure 6. Mean monthly concentrations of NH_4-N, NO_3-N and Bray P in surface collected casts from Florence (4A) and Benfield (4B) soils at a Kansas tallgrass prairie site (from James 1991).

D. Water and Solute Transport

A final aspect to consider is the effect of earthworms on water and solute movement in soils. Earthworm burrows may create preferential flow pathways in the soil profile which alter water balance and water movement (See Tomlin et al. (Chapter 7) this volume). These changes can have important consequences for movement of solutes in soils, and leaching of nutrients and pesticides into subsurface soil and ground water below agroecosystems. Zachmann and Linden (1989) found that *L. rubellus* could significantly increase the depth to which surface applied bromide moved, although the effect was dependent on the presence of surface applied corn residues. They concluded that *L. rubellus* forms stable burrows with many surface openings when surface residues are present, and that these burrows can decrease surface runoff and increase infiltration. Anecic species, which form well-developed vertical burrows up to several meters deep, may be particularly important in creating macropores which can channel water and solutes deep into the soil profile (Edwards et al. 1989, 1992). By increasing infiltration rates earthworms may reduce overland flow and associated losses of soil and nutrients. In one of the few studies investigating the effects of earthworms on overland transport of nutrients, Sharpley et al. (1979) observed increased losses of N and P in surface runoff in New Zealand pastures treated with carbaryl to eliminate earthworms, compared to untreated pastures where earthworms were present. Removal of earthworms resulted in a two-fold increase in volume of surface runoff, and even higher proportional increases in loss of dissolved inorganic N and P. In contrast, the transport of particulate P in surface runoff was greater in pastures where earthworms were present, and was associated with increased sediment transport in the presence of surface casting earthworms. Thus, an assessment of the net effect of earthworms on hydrologic export of nutrients should include effects on both surface and subsurface flows.

VII. Summary

It is surprising how little is actually known about the net effects of earthworms on the biogeochemistry of terrestrial ecosystems in North America. As we have illustrated, there have been some excellent studies on the roles of earthworms in various aspects of nutrient cycling processes in North America and elsewhere. Certainly because of ease, convenience, and practicality, many earthworm researchers have concentrated on earthworm effects at the microsite level with studies conducted over relatively short time scales, often in artificial laboratory microcosms. In our discussion of the effects of earthworms on microbial abundance, composition, activity, and nutrient transformations in casts, we have attempted to draw some general conclusions, such as the tendency for nutrient availability and microbial activity to be enhanced in casts, compared to bulk soil. However, it is possible to find contradictory evidence for almost every parameter examined. This is not for lack of good experimental data, but rather because results are dependent on the species of earthworm studied, as well as a host of other variables (soil type, physicochemical variables, organic matter availability, etc.), and the spatiotemporal scale at which measurements were made.

While earthworms clearly influence transformations of organic matter and nutrients in the soil, the relationships of these effects to ecosystem-level nutrient fluxes, and long-term accumulation or loss of nutrients, are not well understood. It appears that earthworms contribute to nutrient cycling processes in ways that can lead to either increased loss or increased storage of nutrients. Considering carbon, for example, the effect of earthworms usually is to accelerate the breakdown of coarse organic matter and contribute directly and indirectly to increased soil respiration, processes leading to loss of C from the system. But evidence also exists that egestion of C in casts can lead to increased storage through protection of organic matter in stable aggregates and by binding with clays. With regard to nitrogen, earthworms may increase N uptake by microbes and plants, alter the timing and location of N availability, and perhaps even increase N inputs to the system by fixation. However, there also is evidence that earthworm activity contributes to system loss of N through denitrification, volatilization, erosion, and leaching. Ultimately, the most important question regarding the influence of earthworms on biogeochemistry and ecosystem structure and function may be how they influence the balance between processes leading to loss and storage of C and other nutrients.

VIII. Research Imperatives

Spatially and temporally explicit studies of the effects of earthworms on biogeochemical processes are needed at a variety of scales, from the earthworm gut to ecosystem-level effects, and in a variety of ecosystem types. Several general questions to be addressed include: How do earthworms alter the spatial and temporal scales at which nutrient cycling processes occur? What is the relative importance of short-term effects (i.e., rapid recycling of N) and longer-term effects (i.e., storage of C and N) of earthworm activity? How important are microsite effects to overall ecosystem function? A difficult challenge will be the integration of studies across a range of scales to adequately address both mechanistic explanations of the effects of earthworms on nutrient transformations and ecosystem-level consequences of earthworm activity for biogeochemical cycling. Some specific areas in which further research is needed are listed below.

A. Gut Physiology and Biochemistry

Further research is needed on the physiological and biochemical transformations taking place in the earthworm gut, especially as they relate to changes in nutrient availability and microbial processes in casts. Specific gaps include information on C and N assimilation efficiencies of earthworm species with different feeding preferences, and further data on primary sources of C and nutrients for earthworms (i.e., bacteria, fungi, specific organic fractions). Also, further research focusing on the calcium relationships of earthworms, and the relationship of calcium release to availability of other nutrients should be explored.

B. Functional Groups

Further studies of the species-specific effects of earthworms at different scales are needed, and could lead to a redefinition of functional groups in earthworms. There is already considerable evidence that different earthworm species have dissimilar effects on soil structure and nutrient transformations. This raises some important questions about the functional similarities of earthworms grouped into broad ecological categories. Are there better ways of defining ecological categories of earthworms? Do the same functional groupings apply to both temperate and tropical ecosystems?

C. Native Species

More studies of the effects of native species, and comparisons of the roles of native and introduced species where both occur, are needed. Even the basic ecology of most native North American earthworms is poorly known. James (1991) has demonstrated that in tallgrass prairie ecosystems, native North American earthworms can affect nutrient cycling processes differently than introduced European species. Because the displacement of native species by exotics is a relatively recent, and sometimes ongoing, phenomenon (see Kalisz and Wood, Chapter 5, this volume), this should be explored in other ecosystems types.

D. Isotope Studies

Expanded use of stable and radioactive isotopes are needed in both field and laboratory experiments. Use of enriched materials (^{13}C, ^{14}C, ^{32}P, and ^{15}N) has been an effective tool for determining the effects on earthworms on the fate on organic substrates and pathways of nutrient transformation (Cortez et al. 1989, Spain et al. 1992, Binet and Trehen 1992). Analysis of $\delta^{13}C$ values of earthworm tissue has provided some unique insights into the utilization of specific organic matter pools by earthworms in temperate European and tropical ecosystems (Martin et al. 1992a, b). There appear to be opportunities for similar studies in many North American ecosystems, which could provide further insights into the relationships of earthworms with specific organic matter fractions.

E. Nutrient Availability

Studies of the relationship between earthworm activity and spatial and temporal patterns of nutrient availability are needed, particularly in temperate North American ecosystems. We have pointed out several ways in which earthworms influence rates of nutrient transformation and patterns of nutrient availability at the microsite level. The net effect of these microsites on spatiotemporal patterns of nutrient availability in the field and potential for nutrient loss from ecosystems remains largely uninvestigated. Two specific areas requiring further research are the effects of earthworm activity on gaseous N fluxes (N fixation, volatilization, and denitrification) and the role of earthworm casting in aggregate formation and persistence in relationship to storage of C and N. Additionally, research directed at the effects of earthworms on elements other than C and N is needed.

F. Plant Growth

Quantitative studies of the effects of earthworms on plant growth and productivity under field conditions are needed. Earthworm-microbial-rhizosphere interactions seem to have particular promise for future studies. Indications that earthworm activity can be concentrated in the rhizosphere and the potential significance of root herbivory by earthworms should be examined.

G. Interactions with Soil Biota

Earthworms have the potential to affect other components of the soil community in many ways, thereby altering both the structure and function of decomposer food webs and, presumably, nutrient transformations mediated by the decomposer community. To date there have been few studies which have examined simultaneously the effects of earthworms on microbial and invertebrate populations and activity. Further research into the effects of earthworms on soil microbial and invertebrate communities is recommended.

H. Spatial Scales

Appropriate techniques for scaling up from effects observed at the microsite (i.e., casts and burrow linings) to effects on whole soil structure and function are needed. Extrapolation of results from microsites or laboratory incubations to field-scale estimates of nutrient flux will require innovative approaches. Quantification of the densities of specific microsites, and rates of cast, burrow and midden production and disappearance, in different ecosystem types may be required. In addition, landscape-level approaches which explicitly consider the interactions of earthworms with factors such as soil type, texture and resource quality may be particularly useful in scaling from the microsite to the ecosystem or landscape level.

I. Long Term Studies

Finally, there is a definite need for further long-term manipulative field experiments (eliminations, additions) to assess the net effects of earthworms on SOM and nutrient dynamics in a variety of ecosystem types. As indicated in this chapter and in other reviews, there are considerable data on the shorter-term effects of earthworms at the microsite level, and on soils and soil-plant relationships in laboratory and greenhouse incubations. There is much less information on the extent to which these effects occur in the field, their magnitude and their importance to ecosystem-level nutrient fluxes. We suggest that these questions will be adequately addressed only through the use of field experiments in which entire earthworm communities are manipulated for an extended time. We are aware of such experiments currently being done in Ohio, Georgia, and La Mancha, Mexico, in North America. All of these studies are being done in agricultural ecosystems, and there is a need for similar studies to be initiated in other ecosystem types. In addition to manipulating pre-existing earthworm communities, it may be possible to find areas in North America where reintroduction of earthworms following glaciation is ongoing (see James, Chapter 2, this volume). In these areas, studies of long-term changes following reintroduction of earthworms could provide new insights into the net effects of earthworms on a variety of ecosystem properties and processes.

Acknowledgments

We thank G.G. Brown for his input during revision of the manuscript. Support for preparation of this chapter was provided, in part, by NSF grant DEB-9020461. Contribution no. 94-429-B from the Kansas Agricultural Experiment Station.

References

Adu, J.K. and J.M. Oades. 1978. Utilization of organic materials in soil aggregates by bacteria and fungi. *Soil Biol. Biochem.* 10:117–122.

Anderson, J.M. 1988. Spatiotemporal effects of invertebrates on soil processes. *Biol. Fertil. Soils* 6:216–227.

Atlavinyte, O. and J. Dačiulyte. 1969. The effect of earthworms on the accumulation of vitamin B_{12} in soil. *Pedobiologia* 9:165–170.

Bamforth, S.S. 1988. Interactions between protozoa and other organisms. *Agric. Ecosys. Environ.* 24:229–234.

Barois, I. 1992. Mucus production and microbial activity in the gut of two species of *Amynthas* (Megascolecidae) from cold and warm tropical climates. *Soil Biol. Biochem.* 24:1507–1510.

Barois, I. and P. Lavelle. 1986. Changes in respiration rate and some physicochemical properties of a tropical soil during transit through *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). *Soil Biol. Biochem.* 18:539–541.

Barois, I., B. Verdier, P. Kaiser, A. Mariotti, P. Rangel, and P. Lavelle. 1987. Influence of the tropical earthworm *Pontoscolex corethrurus* (Glossoscolecidae) on the fixation and mineralisation of nitrogen. p. 151–158. In: Bonvicini Pagliai, M. and P. Omodeo (eds.) *On earthworms*. A. Mucchi, Bologna, Italy.

Basker, A., A.N. Macgregor, and J.H. Kirkman. 1992. Influence of soil ingestion by earthworms on the availability of potassium in soil: An incubation experiment. *Biol. Fertil. Soils* 14:300–303.

Baylis, J.P., J.M. Cherrett, and J.B. Ford. 1986. A survey of the invertebrates feeding on living clover roots (*Trifolium repens* L.) using ^{32}P as a radiotracer. *Pedobiologia* 29:201–208.

Bhatnagar, T. 1975. Lombricienes et humification: Un aspect nouveau de l'incorporation microbienne d'azote induite par les vers de terre. p. 169–182. In: Gilbertus, K., O. Reisinger, A. Mourey, and J.A. Cancela de Fonseca (eds.) *Biodégradation et humification*. Pierron, Sarreguemines.

Binet, F. and P. Trehen. 1992. Experimental microcosm study of the role of *Lumbricus terrestris* (Oligochaeta: Lumbricidae) on nitrogen dynamics in cultivated soils. *Soil Biol. Biochem.* 24:1501–1506.

Blair, J.M., P.J. Bohlen, C.A. Edwards, B.R. Stinner, D.A. McCartney, and M.F. Allen. (in press) Manipulation of earthworm populations in field experiments in agroecosystems. *Acta Zoologica Fennica*.

Bolton, P.J. and J. Phillipson. 1976. Burrowing, feeding, egestion and energy budget of *Allolobophora rosea* (Savigny) (Lumbricidae). *Oecologia (Berlin)* 23:225–245.

Bouché, M.B. 1975. Action de la faune sur les états de la matierère organique dans les écosystèmes. p. 157–168. In: Gilbertus, K., O. Reisinger, A. Mourey, and J.A. Cancela da Fonseca (eds.) *Biodégradation et humification*. Pierron, Sarruguemines.

Bouché, M.B. 1977. Stratégies lombriciennes. In: Lohm, U. and T. Persson (eds.) *Soil organisms as components of ecosystems*. Ecological Bulletin (Stockholm) 25:122–132.

Christensen, O. 1988. The direct effects of earthworms on nitrogen turnover in cultivated soils. *Ecological Bulletin* 39:41–44.

Coleman, D.C. 1985. Through a ped darkly: an ecological assessment of root-soil-microbial-faunal interactions. p. 1–21. In: Fitter, A.H., D. Atkinson, D.J. Read, and

M.B. Usher (eds.) *Ecological interactions in soil*. Blackwell Scientific Publishing, London.

Cortez, J. and M.B. Bouché. 1992. Do earthworms eat living roots? *Soil Biol. Biochem.* 24:913–915.

Cortez, J., R. Hamheed, and M.B. Bouché. 1989. C and N transfer in soil with or without earthworms fed with ^{14}C- and ^{15}N-labelled wheat straw. *Soil Biol. Biochem.* 21:491–497.

Crossley, D. A. Jr., R.E. Reichle, and C.A. Edwards. 1971. Intake and turnover of cesium by earthworms (Lumbricidae). *Pedobiologia* 11:71–76.

Darwin, C. 1881. *The formation of vegetable mould through the action of worms with observations on their habits*. Faber and Faber, London.

Dash, M.C., B.K. Senapati, and P.C. Mishra. 1980. Nematode feeding by tropical earthworms. *Oikos* 34:322–325.

Dickschen, F. and W. Topp. 1987. Feeding activities and assimilation efficiencies of *Lumbricus rubellus* (Lumbricidae) on a plant only diet. *Pedobiologia* 30:31–37.

Dkhar, M.S. and R.R. Mishra. 1986. Microflora in earthworm casts. *J. Soil Biol. Ecol.* 6:24–31.

Edwards, C.A. and J.R. Lofty. 1977. *Biology of earthworms*. 2nd ed. Chapman and Hall, London.

Edwards, W.M., M.J. Shipitalo, L.B. Owens, and L.B. Norton. 1989. Water and nitrate movement in earthworm burrows within long-term no-till corn fields. *J. Soil Water Cons.* 44:240–243.

Edwards, W.M., M.J. Shipitalo, S.J. Traina, C.A. Edwards, and L.B. Owens. 1992. Role of *Lumbricus terrestris* (L.) burrows on quality of infiltrating water. *Soil Biol. Biochem.* 24:1683–1689.

Ellenby, C. 1945. Influence of earthworms on larval emergence in the potato root eelworm *Heterodera rostochiensis* Wollenweber. *Ann. Appl. Biol.* 31:332–339.

Elliott, P.W., D. Knight, and J.M. Anderson. 1990. Denitrification in earthworm casts and soil from pasture under different fertilizer and drainage regimes. *Soil Biol. Biochem.* 22:601–605.

Elliott, P.W., D. Knight, and J.M. Anderson. 1991. Variables controlling denitrification from earthworm casts and soil in permanent pasture. *Biol. Fertil. Soils* 11:24–29.

Ferriere, G. and M.B. Bouché. 1985. Première mesure écophysiologique d'un débit d'azote de *Nicodrilus longus* (Ude) (*Lumbricidae* Oligochaeta) dans la prairie de Citeaux. *CR Academy Science* 301:789–794.

Hamilton, W.E. and D.Y. Sillman. 1989. Influence of earthworm middens on the distribution of soil microarthropods. *Biol. Fertil. Soils* 8:279–284.

Hendrix, P.F., D.A. Crossley Jr., D.C. Coleman, R.W. Parmelee, and M.H. Beare. 1987. Carbon dynamics in soil microbes and fauna in conventional and no-tillage agroecosystems. *INTECOL Bulletin* 15:59–63.

Hoogerkamp, M., H. Rogaar, and H.J.P. Eijsackers. 1983. Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. p. 85–105. In: Satchell, J.E. (ed.) *Earthworm ecology. From Darwin to vermiculture*. Chapman and Hall, New York.

Hopp, H. and C.S. Slater. 1949. The effect of earthworms on the productivity of agricultural soil. *J. Agric. Res.* 78:325–339.

James, S.W. 1991. Soil, nitrogen, phosphorus, and organic matter processing by earthworms in tallgrass prairie. *Ecology* 72:2101–2109.

James, S.W. and M.R. Cunningham. 1989. Feeding ecology of some earthworms in Kansas tallgrass prairie. *Am. Midl. Nat.* 121:78–83.

James, S.W. and T.R. Seastedt. 1986. Nitrogen mineralization by native and introduced earthworms: Effects on big bluestem growth. *Ecology* 67:1094–1097.

Judas, M. 1992. Gut content analysis of earthworms (Lumbricidae) in a beechwood. *Soil Biol. Biochem.* 24:1413–1417.

Ketterings, Q.M. 1992. Effects of earthworm activities on soil structure stability and soil carbon and nitrogen storage in organic-based and conventional agroecosystems. M.Sc. thesis, Wageningen Agricultural University, The Netherlands. 136 pp.

Knight, D., P.W. Elliott, J.M. Anderson, and D. Scholefield. 1992. The role of earthworms in managed, permanent pastures in Devon, England. *Soil Biol. Biochem.* 24:1511–1518.

Krishnamoorthy, R.V. 1990. Mineralization of phosphorus by faecal phosphatases of some earthworms of Indian tropics. *Proc. Indian Acad. Sci. (Animal Sci.)* 99:509–518.

Krishnamoorthy, R.V. and S.N. Vajranabhaiah. 1986. Biological activity of earthworm casts: an assessment of plant growth promoter levels in the casts. *Proc. Indian Acad. Sci. (Animal Sci.)* 95:341–351.

Lavelle, P. 1988. Earthworm activities and the soil system. *Biol. Fertil. Soils* 6:237–251.

Lavelle, P. and A. Martin. 1992. Small-scale and large-scale effects of endogeic earthworms on soil organic matter dynamics in soils of the humid tropics. *Soil Biol. Biochem.* 24:1491–1498.

Lavelle, P., G. Melendez, B. Pashanasi, and R. Schaefer. 1992. Nitrogen mineralization and reorganization in casts of the geophagous tropical earthworm *Pontoscolex corethrurus* (Glossoscolecidae). *Biol. Fertil. Soils* 14:49–53.

Lavelle, P., B. Sow, and R. Schaefer. 1980. The geophagous earthworm community in the Lamto savanna (Ivory Coast): niche partitioning and utilization of soil nutritive resources. p. 653–672. In: Dindal, D. (ed.) *Soil biology as related to land use practices*. EPA, Washington, D.C.

Lee, K.E. 1985. *Earthworms: their ecology and relationships with soils and land use.* Academic Press, New York.

Lopez-Hernandez, D., P. Lavelle, J.C. Fardeau, and M. Niño. 1993. Phosphorus transformations in two-P-sorption contrasting tropical soils during transit through *Pontoscolex corethrurus* (Glossoscolecidae: Oligochaeta). *Soil Biol. Biochem.* 25:789–792.

Lunt, H.A. and G.M. Jacobson. 1944. The chemical composition of earthworm casts. *Soil Sci.* 58:367–375.

Mackay, A.D. and E.J. Kladivko. 1985. Earthworms and rate of breakdown of soybean and maize residues in soil. *Soil Biol. Biochem.* 17:851–857.

Marinissen, J.C.Y. and J. Bok. 1988. Earthworm-amended soil structure: Its influence on Collembola populations in grassland. *Pedobiologia* 32:243–252.

Martin, A. 1991. Short- and long-term effects of the endogeic earthworm *Millsonia anomala* (Omodeo) (Megascolicidae, Oligochaeta) of tropical savannas, on soil organic matter. *Biol. Fertil. Soils* 11:234–238.

Martin, A., J. Balesdent, and A. Mariotti. 1992b. Earthworm diet related to soil organic matter dynamics through ^{13}C measurement. *Oecologia* 91:23–29.

Martin, A. and J.C.Y. Marinissen. 1993. Biological and physico-chemical processes in excrements of soil animals. *Geoderma* 56:331–347.

Martin, A., A. Mariotti, J. Balesdent, and P. Lavelle. 1992a. Soil organic matter assimilation by a geophagous tropical earthworm based on $\delta^{13}C$ measurements. *Ecology* 73:118–128.

Nielson, R.L. 1965. Presence of plant growth substances in earthworms demonstrated by paper chromatography and the Went pea test. *Nature* 208:113–114.

Park, S.C., T.J. Smith, and M.S. Bisesi. 1992. Activities of phosphomonoesterase and phosphodiesterase from *Lumbricus terrestris*. *Soil Biol. Biochem.* 24:873–876.

Parle, J.N. 1963. Microorganisms in the intestines of earthworms. *J. Gen. Microbiol.* 31:1–11.

Parmelee, R. W., M.H. Beare, W. Cheng, P.F. Hendrix, S.J. Rider, D.A. Crossley Jr., and D.C. Coleman. 1990. Earthworms and enchytraeids in conventional and no-tillage agroecosystems: A biocide approach to assess their role in organic matter breakdown. *Biol. Fertil. Soils* 10:1–10.

Parmelee, R.W. and D.A. Crossley, Jr. 1988. Earthworm production and role in the nitrogen cycle of a no-tillage agroecosystem on the Georgia piedmont. *Pedobiologia* 32:351–361.

Satchell, J. E. 1963. Nitrogen turnover by a woodland population of *Lumbricus terrestris*. p. 60–66. In: Doeksen, J. and J. van der Drift (eds.) *Soil organisms*. North-Holland Publishing Co., Amsterdam.

Satchell, J.E. 1967. Lumbricidae. p. 259–322. In: Burges, A. and F. Raw (eds.) *Soil biology*. Academic Press, London.

Satchell, J.E. (ed.) 1983. *Earthworm ecology. From Darwin to vermiculture.* Chapman and Hall, New York.

Satchell, J.E. and K. Martin. 1984. Phosphatase activity in earthworm faeces. *Soil Biol. Biochem.* 16:191–194.

Scheu, S. 1987. Microbial activity and nutrient dynamics in earthworm casts (Lumbricidae). *Biol. Fertil. Soils* 5:230–234.

Shapiro, D.I., E.C. Berry, and L.C. Lewis. 1993. Interactions between nematodes and earthworms: Enhanced dispersal of *Steinernema carpocapsae*. *J. Nematology* 25:189–192.

Sharpley, A.N. and J.K. Syers. 1976. Potential role of earthworm casts for the phosphorus enrichment of runoff waters. *Soil Biol. Biochem.* 8:341–346.

Sharpley, A.N., J.K. Syers, and J.A. Springett. 1979. Effect of surface-casting earthworms on the transport of phosphorus and nitrogen in surface runoff from pasture. *Soil Biol. Biochem.* 11:459–462.

Shaw, C. and S. Pawluk. 1986a. Faecal microbiology of *Octolasion tyrtaeum*, *Aporrectodea turgida* and *Lumbricus terrestris* and its relation to carbon budgets of three artificial soils. *Pedobiologia* 29:377–389.

Shaw, C. and S. Pawluk. 1986b. The development of soil structure by *Octolasion tyrtaeum*, *Aporrectodea turgida* and *Lumbricus terrestris* in parent materials belonging to different textural classes. *Pedobiologia* 29:327–339.

Shipitalo, M.J. and R. Protz. 1988. Factors influencing the dispersability of clay in worm casts. *Soil Sci. Soc. Am. J.* 52:764–769.

Šimek, M. and V. Pižl. 1989. The effects of earthworms (Lumbricidae) on nitrogenase activity in soil. *Biol. Fertil. Soils* 7:370–373.

Spain, A. V., P. Lavelle, and A. Mariotti. 1992. Stimulation of plant growth by tropical earthworms. *Soil Biol. Biochem.* 24:1629–1633.

Spiers, G.A., D. Gagnon, G.E. Nason, E.C. Packee, and J.D. Lousier. 1986. Effects and importance of indigenous earthworms on decomposition and nutrient cycling in coastal forest ecosystems. *Can. J. For. Res.* 16:983–989.

Springett, J.A. and J.K. Syers. 1979. The effect of earthworm casts on ryegrass seedlings. p. 44–47. In: Crosby, T.K., and R.P. Pottinger (eds.) *Proc. 2nd Australasian Conf. Grassland Invert. Ecol.* Government Printer, Wellington, New Zealand.

Stockdill, S.M.J. 1982. Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia* 24:29–35.

Svensson, B.H., U. Boström, and L. Klemedston. 1986. Potential for higher rates of denitrification in earthworm casts than in the surrounding soil. *Biol. Fertil. Soils* 2:147–149.

Syers, J. K., A.N. Sharpley, and D.R. Keeney. 1979. Cycling of nitrogen by surface-casting earthworms in a pasture ecosystem. *Soil Biol. Biochem.* 11:181–185.

Tiwari, S.C., B.K. Tiwari, and R.R. Mishra. 1989. Microbial populations, enzyme activities and nitrogen-phosphorus-potassium enrichment in earthworm casts and in the surrounding soil of a pineapple plantation. *Biol. Fertil. Soils* 8:178–182.

Tomati, U., A. Grappelli, and E. Galli. 1988. The hormone-like effect of earthworm casts on plant growth. *Biol. Fertil. Soils* 5:288–294.

Trigo, D. and P. Lavelle. 1993. Changes in respiration rate and some physicochemical properties of soil during gut transit through *Allolobophora molleri* (Lumbricidae, Oligochaeta). *Biol. Fertil. Soils* 15:185–188.

West, L.T., P.F. Hendrix, and R.R. Bruce. 1991. Micromorphic observations of soil alteration by earthworms. *Agric. Ecosystems Environ.* 34:363–370.

Wolters, V. and R.G. Joergensen. 1992. Microbial carbon turnover in beech forest soils worked by *Aporrectodea caliginosa* (Savigny) (Oligochaeta: Lumbricidae). *Soil Biol. Biochem.* 24:171–177.

Yeates, G. W. 1981. Soil nematode populations depressed in the presence of earthworms. *Pedobiologia* 22:191–195.

Zachmann, J.E. and D.R. Linden. 1989. Earthworm effects on corn residue breakdown and infiltration. *Soil Sci. Soc. Am. J.* 53:1846–1849.